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Female- and male-specific signals of quality in the barn owl

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Abstract

Most bird studies of female signalling have been confined to species in which females display a male-ornament in a vestigial form. However, a great deal of benefit may be gained from considering phenotypic traits that are specific to females. This is because (1) sex-specific traits may signal sex-specific qualities and (2) females may develop a male-ornament not because they are selected to do so, but because fathers transmit to daughters the underlying genes for its expression (genetic correlation between the sexes). We investigated these two propositions in the barn owl *Tyto alba*, a species in which male plumage is lighter in colour and less marked with black spots than that of females. Firstly, we present published evidence that female plumage spottiness reflects parasite resistance ability. We also show that male plumage coloration is correlated with reproductive success, male feeding rate and heart mass. Secondly, cross-fostering experiments demonstrate that plumage coloration and spottiness are genetically correlated between the sexes. This implies that if a given trait value is selected in one sex, the other sex will indirectly evolve towards a similar value. This prediction is supported by the observation that female plumage coloration and spottiness resembled that of males, in comparisons at the level of *Tyto alba alba* populations, *Tyto alba* subspecies and *Tyto* species. Our results therefore support the hypothesis that sex-specific traits signal sex-specific qualities and that a gene for a sex-specific trait can be expressed in the other sex as the consequence of a genetic correlation between the sexes.

Introduction

The study of the function of female plumage attributes has recently attracted the attention of evolutionary biologists (Amundsen, 2000). This growing interest emerged because empirical data do not firmly support the theoretical expectation that under a wide range of conditions females may be under sexual selection to develop striking plumage traits (Trivers, 1972; Owens & Thompson, 1994; Johnstone *et al*., 1996). In birds, only a handful of studies reported significant relationships between fitness components and the extent to which females display a plumage ornament (Amundsen, 2000). However, because research in birds has focused on traits expressed to a lesser degree in females than in males, a statement about how frequently females signal quality with a plumage trait cannot yet be given. A posteriori, the aim of these studies was to assess whether a male-ornament has a signal function in females rather than to determine whether females signal quality by displaying a plumage trait. Therefore, the study of female ornamentation would benefit from considering not only male-ornament but other phenotypic traits as well.

Determinants of ornament size can be identical in males and females (Hill, 1993; Roulin *et al*., 1998) implying that an ornament can reveal a similar quality in both sexes. For example, in the barn swallow (*Hirundo rustica*) both longer-tailed males and females

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produce more offspring (Møller, 1994). However, there may be some traits that occur in males and females, but that are sex-specific signals reflecting different qualities that do not necessarily correlate with each other (Wedekind, 1992; Møller & Pomiankowski, 1993; Johnstone, 1995). For instance, in sticklebacks (*Gasterosteus aculeatus*) males take care of the eggs, and hence male traits may signal the quality of paternal care (Künzler & Bakker, 2000), whereas female traits may signal fecundity (Kraak & Bakker, 1998). This example emphasizes the possibility that females and males may signal different qualities with different phenotypic traits.

Another reason to consider sex-specific traits while investigating signals of sex-specific quality, is that a covariation between a fitness component and a male-ornament within females does not necessarily imply that females are under selection to display the male-ornament (Møller, 1993 vs. Cuervo *et al.*, 1996). In the instance that fathers transmit to daughters the underlying genes coding for both a male-ornament and its associated quality, the covariation between these two characteristics within females might be merely the result of a genetically correlated response to selection on males (Halliday & Arnold, 1987). A more stringent support for the hypothesis that females are selected to signal a quality by displaying a phenotypic trait would be given if one discovers a trait which is more extravagantly expressed in females and reveals quality more accurately amongst females than males (but see Jones & Hunter, 1999). This would suggest that females rather than males are under selection to signal quality by displaying such a trait.

Consideration of sex-specific traits therefore appears to be important in the detection of sex-specific signals of quality. A species that is especially suited for such an investigation is the barn owl (*Tyto alba*). Plumage varies in coloration from dark reddish-brown to white and in spottiness from immaculate to heavily marked with black spots. Members of both sexes can display any phenotype, and males are on average lighter coloured and females more spotted (Roulin, 1999a). Plumage coloration and spottiness varies greatly not only within population (Roulin, 1999b), but also among 36 worldwide distributed *Tyto alba* subspecies and seven *Tyto* species (Taylor, 1994). In the present study, we tested four predictions of the hypothesis that sex-specific traits advertise sex-specific qualities and yet are expressed in both sexes because of genetic correlation between the sexes. One of the predictions has already been published in a series of three papers showing that females may be under sexual selection to exhibit plumage spottiness (Roulin, 1999b) and that female plumage spottiness signals her offspring's ability to resist parasites (Roulin *et al.*, 2000, 2001). In the present paper, we report results of the other three predictions.

Prediction 1: male plumage coloration reflects male parental care

As males do most of the hunting from courtship feeding until the end of the breeding season (Roulin, 1999b), males may be selected to signal the amount of parental care they can perform. Because plumage becomes lighter coloured from the first- to the second-year of age and males are lighter coloured than females (Roulin, 1999a), we predict that male plumage coloration reflects parental care and in turn brood success. Additionally, given that a large heart may be required to sustain intense feeding effort, or alternatively, given that intense feeding effort may lead to the development of a large heart (e.g. Harris *et al.*, 1995; Duncan *et al.*, 1998), we also predict that heart size covaries with plumage coloration.

Prediction 2: plumage spottiness and coloration are genetically correlated between the sexes

As plumage coloration and spottiness are heritable (Roulin *et al.*, 1998) and expressed in the two sexes, we predict that they are genetically correlated between the sexes. In this case, cross-fostered offspring and their genetic parents should resemble each other with respect to both plumage traits.

Prediction 3: females and males coevolve with respect to plumage traits

If plumage traits are genetically correlated between the sexes, females and males should coevolve towards similar plumage trait values. We predict that females from a given *Tyto alba alba* population resemble more closely males of the same population than any another. We have a similar expectation when comparing females and males from different *Tyto alba* subspecies and different *Tyto* species.

Methods

Model organism

Barn owls have a high reproductive potential. Clutch size ranges from 2 to 11 (mean = 6.0), brood size from 1 to 9 (mean = 4.1) (personal observation), and in some years up to 64% of breeding pairs produce two broods (Taylor, 1994). As in most predatory birds, the male feeds his partner from prior to egg laying to hatching. He provisions the family alone until offspring are about 2-week-old when his partner starts participating in hunting duties at half his rate (Roulin, 1999b). Offspring fledge at 55 days and are independent at 70–85 days (Cramp & Simmons, 1985). In captivity females stop caring for their offspring before males (Epple, 1985), whereas wild females frequently desert offspring half way through

the nestling period to start a second breeding attempt with a new mate (Roulin, personal observation). In summary, although sex-roles in reproduction are not reversed as in polyandrous species, males appear to invest more effort in reproduction, at least with respect to feeding of the brood.

Studies performed in a Swiss population have shown that plumage spottiness has a signal function in females. In the first of a series of three studies, successive female mates of the same male were similarly spotted and mates of father and sons displayed plumage spottiness to a similar extent. Additionally, mating with respect to this plumage trait was assortative, and paternal investment decreased after plumage spottiness of his female mate was experimentally reduced (Roulin, 1999b). Note that mating with respect to plumage coloration is not assortative (Roulin, 1999b). In a second study, Roulin *et al.* (2000) demonstrated that females that were more spotted produced offspring that were better able to mount a specific antibody response against an immune challenge with sheep red blood cells. In the latest study, blood-sucking flies *Carnus haemapterus* were less abundant on nestlings raised in nests of more heavily spotted females and these flies were also less fecund (Roulin *et al.*, 2001). An experiment where clutches were swapped between nests demonstrated that plumage spottiness of genetic, but not foster mother, predicts low parasite fecundity (Roulin *et al.*, 2001). Furthermore, more heavily spotted females had a smaller bursa of Fabricius, an organ that produces B cells that in turn produce antibodies. This suggests that heavily spotted females are under lower immune challenge. Notably, male plumage spottiness did not appear to signal offspring parasite resistance and to covary with the size of their bursa of Fabricius. Because of these reasons and the fact that female plumage spottiness is heritable (Roulin *et al.*, 1998), males may be choosing females by assessing this trait as an indicator of female genetic quality.

Prediction 1: male plumage coloration reflects male parental care

We investigated the relationship between parental care and plumage coloration in three ways.

Plumage coloration and reproductive success

From 1994 to 2000, reproductive success was recorded in relation to plumage coloration in a Swiss population (46°49′ N/06°56′ E). Pairs were bred in a farmland area covering 190 km^2 in which 110 nest-boxes had been fastened to barns. Each year clutch size, hatching date, and brood size were recorded. Fledging success is given by the ratio 'brood size at fledging divided by brood size at hatching'. Sex of breeding birds was recognized by the presence (female) or absence (male) of a brood patch, and birds were classified as 'yearling' or 'adult' based on ring numbers and moult pattern (Taylor, 1994). This classification is necessary because birds become lighter coloured from the first to the second year of age, but not later on (Roulin, 1999a).

One of the authors (A. R.) compared plumage coloration of the breast, belly, one flank and underside of one wing with eight colour chips that range from one for dark reddish-brown to eight for white. The mean value from the four body parts provided a reliable colour index denoted 'plumage coloration' (Roulin, 1999a). This was measured on 325 breeding males (159 different individuals) and on 353 breeding females (184 different individuals). Fewer males were recorded because of the difficulty in capturing them. To test whether plumage coloration covaries with hatching date, clutch size, and brood size at hatching and fledging, we first removed annual variation in these breeding parameters using a one-way ANOVA. Residual values were saved, and if an individual appeared more than once in the data file, we calculated mean residual values indicating whether, regardless of the year, this individual bred on average early in the season, produced a large clutch and a large brood. For each sex and breeding parameter, we performed a three-way ANOVA with residual breeding parameter as the dependent variable, and plumage coloration, age and plumage spottiness (see below for how this trait was measured) as three independent variables. We controlled for plumage spottiness statistically because this trait covaries with plumage coloration, especially within males (unpublished results).

In order to examine whether a relationship between reproductive success and plumage coloration may be because of the fact that differently coloured birds invest differentially in reproduction or occupy territories of different quality, we determined whether reproductive success was better predicted by the territory in which birds bred or by bird identity. For this purpose, we used data collected between 1988 and 2000. We performed an ANOVA with brood size at fledging as the dependent variable and with year, nest-site and breeder identity as independent variables.

Plumage coloration and feeding rate

A significant relationship between reproductive success and male plumage coloration can be because of a high feeding rate by colourful males or by their mate (e.g. de Lope & Møller, 1993; Roulin, 1999b). For this reason, feeding rate was recorded in 1997 in 28 broods. One week before recording, parents were captured and ringed on a different leg so that gender could be recognized in data videos. An infrared sensitive camera was placed within the nest-box the day before recording feeding activities of the two parents on two successive nights. Feeding rate is reported as mean number of prey items delivered from 21.30 to 05.30 h. Measurements were taken when the first-hatched nestling was 36 ± 6 days of age (range = 18–49 days). Note that feeding rate was

not correlated with nestling age (Pearson correlation, male: $r = 0.07$, $n = 26$, $P = 0.74$; female: $r = -0.04$, $n = 26$, $P = 0.83$). Only six out of 66 yearlings bred in 1997, and as they did not significantly differ in plumage coloration from adults (Student *t*-test: $t = 1.18$, d.f. $= 64$, $P = 0.25$), we did not control for age in the statistical analyses.

Plumage coloration and heart mass

In order to test the prediction that heart mass covaries with plumage coloration, we weighed this organ from 93 barn owls found dead along French highways (regions Champagne and Lorraine). These birds were collected daily between 15 September 1998 and 24 February 2000 and put in a freezer. On 6 and 7 April 2000 plumage coloration was measured (A. R.), body mass weighed after having removed stomach content, and heart mass weighed to the nearest 0.01 g. Sex was determined via gonad inspection and birds classified as 'yearling' or 'adult' depending on whether a bursa of Fabricius was found or not (Glick, 1983). Heart mass did not significantly covary with date of discovery (1 June defined as day 0, $r = 0.17$, $n = 85$, $P = 0.12$).

Prediction 2: plumage spottiness and coloration are genetically correlated between the sexes

The extent to which a resemblance between relatives of opposite sex has a genetic basis was determined via cross-fostering experiments performed in 3 years in the same Swiss population. These experiments were designed to randomize offspring among environments, so that any resemblance between cross-fostered offspring and genetic parents with respect to a plumage trait can be attributed to genetic or prehatching maternal effects. In 1996, among 28 pairs of nests one hatchling of a nest A was exchanged with three same-aged chicks of a nest B. We exchanged a different number of hatchlings between nests to manipulate brood size and in turn the condition of the chicks. Brood size manipulations did not alter the expression of plumage traits (Roulin *et al.*, 1998). In 1998, among 19 pairs of nests half of hatchlings of a nest A was exchanged with the same number of hatchlings of a nest B. As in 1996, we recognized the origin of the nestlings by marking them with nontoxic paint when they were too small to be ringed. In 1999, nests were matched in 17 pairs and the clutch of a nest A was swapped with that of a nest B. More details on these experiments are given elsewhere (Roulin *et al.*, 1998; 2000; 2001). Gender was determined using molecular techniques (Roulin *et al.*, 1999).

Plumage coloration and spottiness were measured on the breast, belly, flanks and underside of the wings of 55-day-old nestlings and their parents. Coloration was scored as explained above. In order to record plumage spottiness, spots were counted within a 60×40 mm^2 frame placed on these four body regions. The diameter of three to 24 spots was measured with a calliper to the nearest 0.1 mm. The percentage of the surface covered by spots was given by the formula $100 \times \pi \times$ number of spots $\times$ (mean spot diameter/2)^2/(60×40). We averaged the percentages of the two flanks (and of the two wings), and subsequently determined the mean percentage from all four body regions. This value was square-root transformed to normalize the data set, denoted 'plumage spottiness', and confirmed to be reliable (Roulin, 1999b).

Genetic correlation between the sexes was estimated by twice the slope of the regression of mean plumage characteristics of all cross-fostered sons (vs. daughters) on plumage characteristics of genetic mother (vs. father). We adjusted estimates for differences in phenotypic variation between the sexes by multiplying the daughter–father regression coefficient with the ratio of mother to father phenotypic standard deviations (ratio for plumage coloration = 1.03; plumage spottiness = 0.86). The son–mother regression coefficient was multiplied with the ratio of father to mother phenotypic standard deviations (ratio for plumage coloration = 0.90; plumage spottiness = 1.20) (Falconer, 1989). Finally, we corrected estimates for assortative mating with the factor $1/(1 + r)$, r being the Pearson correlation coefficient between plumage trait values of breeding partners (Falconer, 1989). We multiplied daughter–father regression coefficients with 0.91 for plumage coloration and with 0.77 for plumage spottiness, and the son–mother coefficient with 0.97 and 0.89, respectively.

Prediction 3: coevolution of female and male plumage characteristics

A. R. measured plumage coloration and spottiness of skins preserved in 44 museums (see Appendix web material) to investigate whether females and males coevolve towards similar plumage trait values at the population, subspecies and species levels. The same method of assessing plumage traits was used except that only the breast and belly could be considered, as flanks and underside of the wings were not visible. Therefore, the mean value of these two body parts was used in the statistical analyses. 4726 skins were handled, but because some skins could not be adequately measured (e.g. skins in deteriorated shape), were not sexed, or their origin or taxonomy was unknown, a sample of 3381 skins was finally considered in the present study (web materials).

Statistics

Statistical tests were computed with the JMP statistical package (Sall & Lehman, 1996). Means are quoted with ±1 SE. *P*-values lower than 0.05 are considered as significant.

Table 1 Relationship between plumage coloration and breeding parameters of breeders captured from 1994 to 2000. Each individual appears only once in the analysis. For each breeding parameter and sex the dependent variable was residual breeding parameter after having removed interannual variation. Independent variables were age, plumage coloration and spottiness. Only the results for plumage coloration are reported.

	Hatching date	Clutch size	Brood size at hatching	Brood size at fledging
Male coloration	$F_{1,156} = 0.25$, $P = 0.62$	$F_{1,150} = 1.69$, $P = 0.20$	$F_{1,149} = 2.04$, $P = 0.16$	$F_{1,155} = 5.25$, $P = 0.02$
Female coloration	$F_{1,180} = 7.03$, $P = 0.01$	$F_{1,177} = 2.03$, $P = 0.16$	$F_{1,173} = 2.49$, $P = 0.12$	$F_{1,177} = 1.83$, $P = 0.18$

Results

Prediction 1: male plumage coloration reflects male parental care

Plumage coloration and reproductive success

Male plumage coloration was significantly correlated with brood size at fledging (Table 1), with more reddish-brown males producing larger broods at fledging (Fig. 1). All other breeding parameters (hatching date, clutch size, and brood size at hatching) did not covary significantly with male plumage coloration (Table 1). The fact that male identity ($F_{148,156} = 1.48$, $P = 0.008$) but not nest-site ($F_{51,156} = 0.78$, $P = 0.85$) predicted brood size after controlling for annual variation ($F_{10,156} = 2.59$, $P = 0.006$) suggests that differently coloured males achieved a different reproductive success because they invest differentially in reproduction rather than because they breed in territories of different quality. With respect to female plumage coloration, we found a significant association with hatching date but not with other breeding parameters (Table 1). Lighter coloured females reproduced earlier in the season (Fig. 2).

Plumage coloration and feeding rate

In 1997, males that were more reddish-brown produced significantly more fledglings (Spearman rank correlation: $r_s = -0.48$, $n = 33$, $P = 0.005$), whereas female plumage coloration was not significantly correlated with brood size at fledging ($r_s = -0.12$, $n = 33$, $P = 0.49$). In an ANCOVA, where male and female feeding rates were entered as repeated measures, male plumage coloration appeared to explain a significant part of the variance ($F_{1,24} = 5.92$, $P = 0.023$) in contrast to female plumage coloration ($F_{1,24} = 1.61$, $P = 0.22$) and hatching date ($F_{1,24} = 0.66$, $P = 0.42$). More reddish-brown males fed their brood at a greater rate (Fig. 3). Note that male plumage coloration was not significantly correlated with clutch size ($r_s = -0.26$, $n = 33$, $P = 0.15$) in contrast to fledging success ($r_s = -0.42$, $n = 33$, $P = 0.016$).

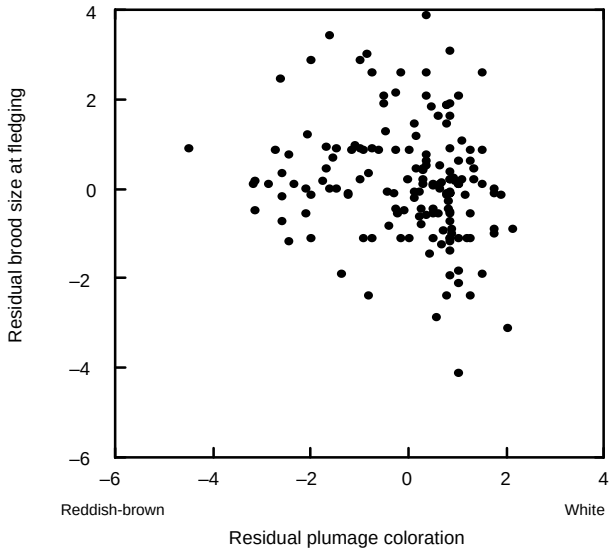

Fig. 1 Relationship between brood size at fledging and male plumage coloration for 159 different males captured between 1994 and 2000. Brood size is expressed as a residual value after having removed interannual variance. Male plumage coloration is expressed as a residual value after having removed variance explained by age and male plumage spottiness.

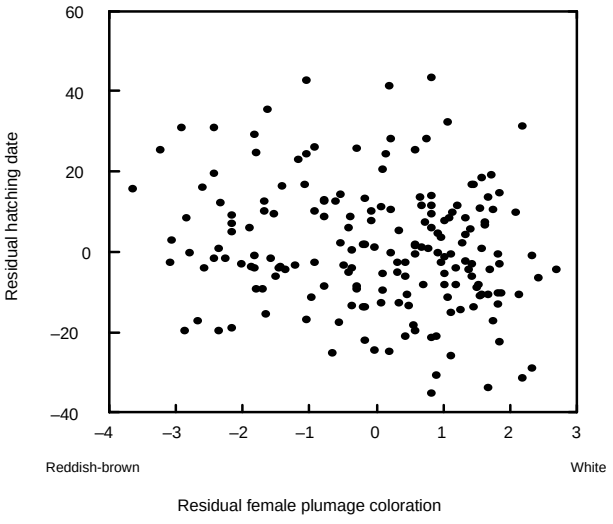

Fig. 2 Relationship between hatching date and female plumage coloration for 184 different females captured between 1994 and 2000. Hatching date is expressed as a residual value after having removed interannual variance. Female plumage coloration is expressed as a residual value after having removed variance explained by age and female plumage spottiness.

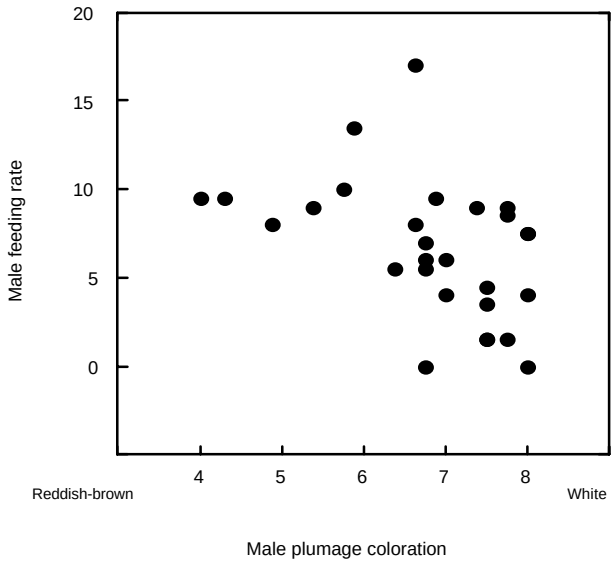

Fig. 3 Male feeding rate in relation to male plumage coloration. Pearson correlation is $r = -0.45$, $n = 28$, $P = 0.017$.

Plumage coloration and heart mass

Heart mass significantly covaried with plumage coloration (ANCOVA, $F = 4.38$, d.f. $= 1, 90$, $P = 0.039$) after controlling for body mass ($F = 33.02$, d.f. $= 1, 90$, $P < 0.001$), sex (females had a heavier heart than males, $F = 7.21$, d.f. $= 1, 90$, $P = 0.009$), and age ($F = 0.06$, d.f. $= 1, 90$, $P = 0.80$; interaction sex by age: $F = 3.10$, d.f. $= 1, 90$, $P = 0.08$). More reddish-brown birds had a heavier heart (Fig. 4).

Prediction 2: plumage spottiness and coloration are genetically correlated between the sexes

Plumage coloration of cross-fostered daughters was significantly correlated with plumage coloration of their genetic father. The same holds true for plumage spottiness. Similar findings apply to the comparison of cross-fostered sons' and genetic mother' plumage characteristics (Table 2).

Prediction 3: coevolution of female and male plumage characteristics

With respect to plumage coloration and spottiness there was a close resemblance between females and males belonging to the same population of the subspecies *Tyto alba alba* (coloration: $r = 0.97$, $n = 7$, $P < 0.001$; spottiness: $r = 0.95$, $n = 7$, $P = 0.001$; Fig. 5). The same findings apply to the comparison of females and males within a *Tyto alba* subspecies (coloration: $r = 0.90$, $n = 22$, $P < 0.001$; spottiness: $r = 0.92$, $n = 22$, $P < 0.001$; Fig. 6). This was also the case at the level of *Tyto* species (coloration: $r = 0.997$, $n = 6$, $P < 0.001$, spottiness: $r = 0.97$, $n = 6$, $P = 0.001$; Fig. 7). Females

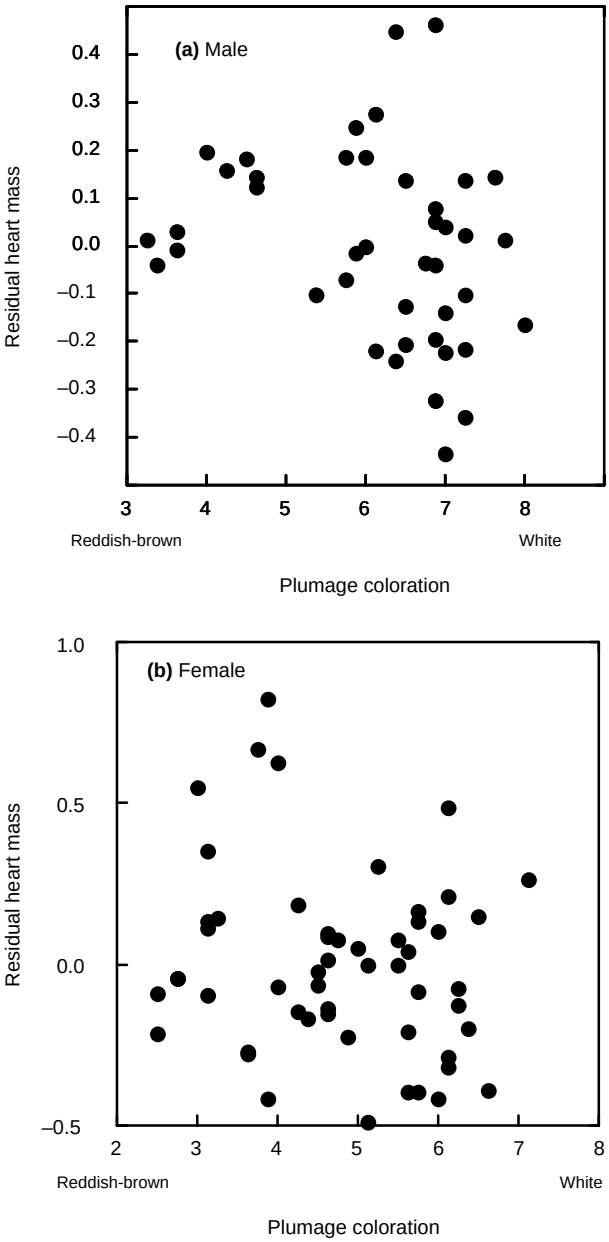

Fig. 4 Relationship between heart mass and plumage coloration of (a) males and (b) females. Residuals are extracted from an ANCOVA including heart mass as dependent variable, age and sex as factors, and body mass as a covariate.

were almost always more reddish-brown and more spotted than males (Figs 5–7).

Discussion

Previous studies in the barn owl have shown that female plumage spottiness advertises the offspring' ability to resist parasites (Roulin, 1999b; Roulin *et al.*, 2000; 2001), and the present study shows that male plumage color-

Table 2 Genetic correlation between the sexes for plumage coloration and spottiness.

	Cross-fostered sons × genetic mother	Cross-fostered daughter × genetic father
Plumage coloration	0.65 ± 0.14; $F_{1,77}$ = 21.5, P < 0.001	0.68 ± 0.16; $F_{1,60}$ = 17.1, P < 0.005
Plumage spottiness	1.01 ± 0.18; $F_{1,77}$ = 29.1, P < 0.001	0.59 ± 0.10; $F_{1,60}$ = 35.0, P < 0.001

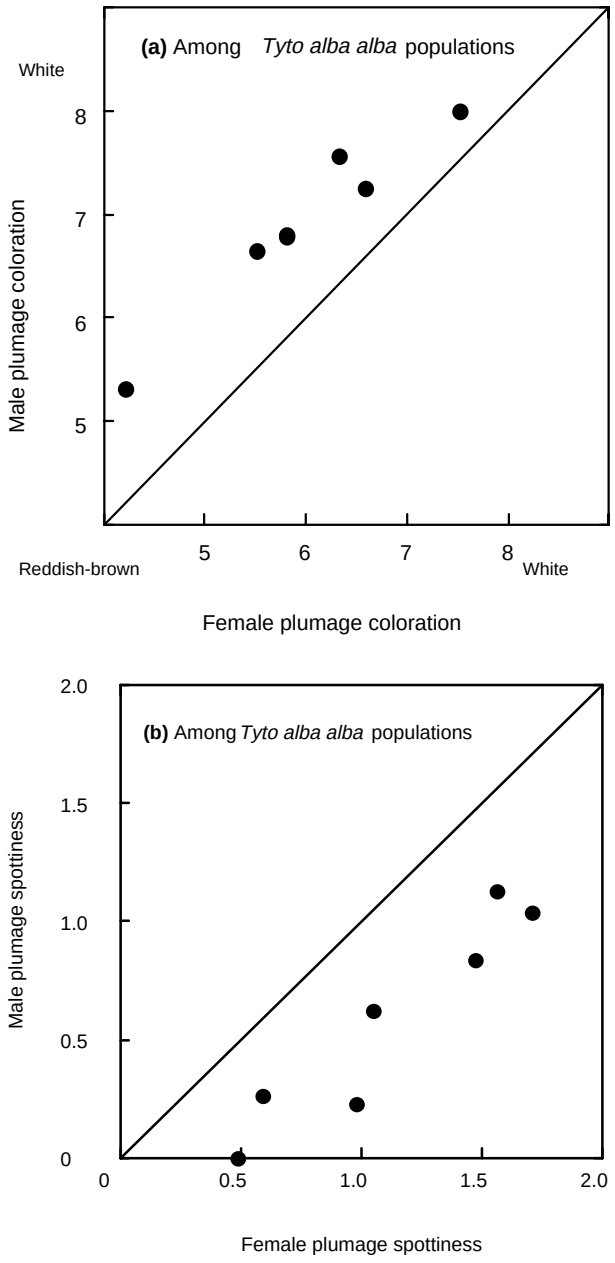

Fig. 5 Relationship between plumage traits of females and males from different European *Tyto alba alba* populations. Each point represents the mean plumage trait value of all males (vs. females) of a given population. (a) Plumage coloration, (b) plumage spottiness. The solid line is the line of equality (males are similarly feathered as females).

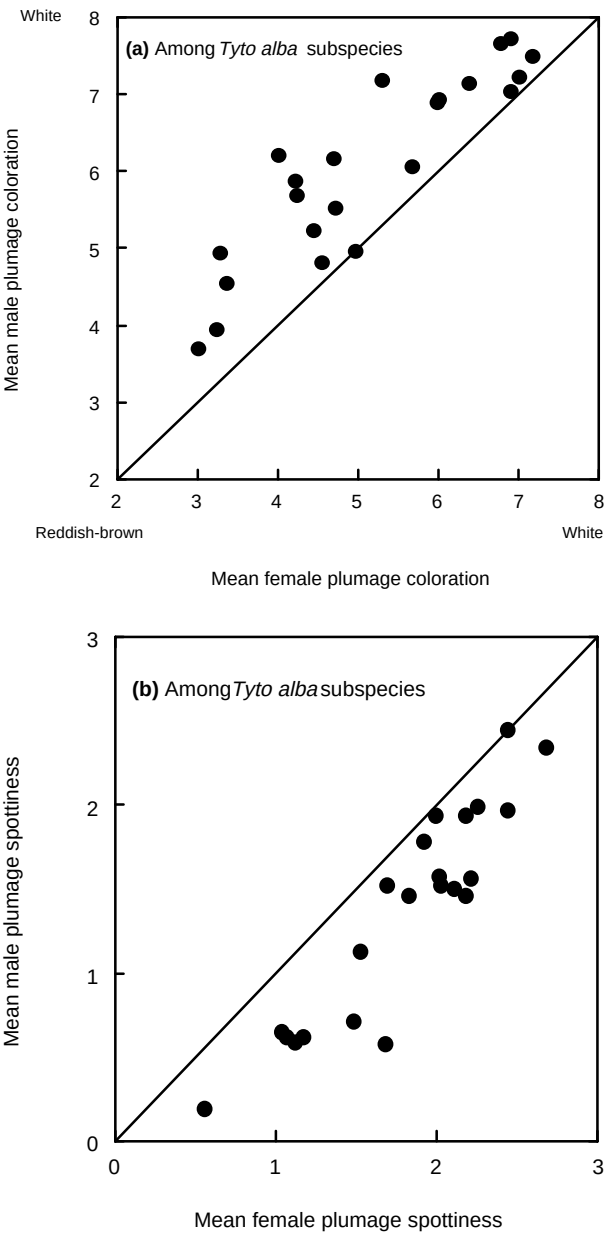

Fig. 6 Relationship between mean plumage coloration (a) and spottiness (b) of females and males of different *Tyto alba* subspecies. Each point represents the mean plumage trait value of all males (vs. females) of a given subspecies. The solid line is the line of equality (males are similarly feathered as females).

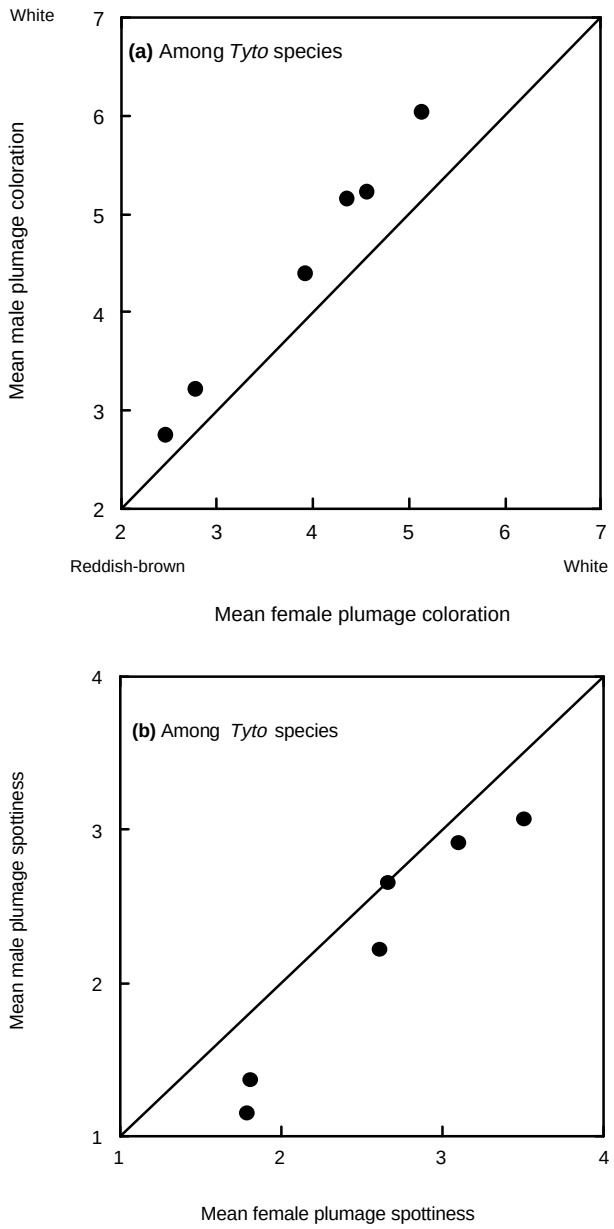

Fig. 7 Relationship between mean plumage coloration (a) and spottiness (b) of females and males of different *Tyto* species. Each point represents the mean plumage trait value of all males (vs. females) of a given species. The solid line is the line of equality (males are similarly feathered as females).

ation is correlated with reproductive success, male feeding rate and heart mass. More data in other birds are required to determine how often sex-specific traits signal sex-specific qualities. To reach this task, future studies may consider plumage traits that are not necessarily exhibited in the most extravagant state (Johnstone, 1996), as the current tendency is to focus exclusively on such traits (Amundsen, 2000).

Genetic correlation between the sexes

To our knowledge, this is the first experimental determination of a genetic correlation between the sexes for plumage traits in any wild bird species. Previous attempts included the comparison of traits displayed by parents and non-cross-fostered offspring of the opposite sex (Møller, 1993; Potti, 1993). Such a comparison suffers the drawback of being unable to disentangle environmental from genetic effects on the resemblance between relatives. This is of importance, as the determination of the magnitude of genetic correlation is crucial in estimating to what extent females express a male-ornament because fathers pass on to daughters genes coding for that trait. A large genetic correlation indicates that a large part of the resemblance between the sexes can be because of indirect selection.

In the barn owl, the intensity of genetic correlation was high for both plumage coloration and plumage spottiness. Maternal effects did not inflate the magnitude of the estimated genetic correlation because mothers do not resemble daughters more than fathers resemble sons with respect to plumage coloration (Roulin *et al.*, 1998; unpublished results). With respect to plumage spottiness, the stronger genetic correlation between mothers and sons being double that of fathers and daughters suggests a sex-linked inheritance with genes of major effect being located on the Z-chromosome (females are heterogametic ZW and males homogametic ZZ). This means that with respect to both plumage coloration and spottiness the resemblance between offspring and parents of opposite sex has a genetic basis. Therefore, if one sex is selected to display a given plumage value, the other sex should indirectly coevolve towards a similar trait value as suggested by the data gathered in museums (Figs 5–7).

Signal function of plumage coloration

Reddish-brown males fed their brood at a higher rate and achieved a higher reproductive success than light coloured males. The observation that the heart was heavier when birds were darker coloured, independently of age, suggests that these birds may be predisposed to invest more effort in reproduction. Three possibilities can account for this suggestion.

1 Dark males are in better condition than light coloured ones. This hypothesis can be rejected because the expression of plumage coloration was shown not to be condition-dependent in nestlings (Roulin *et al.*, 1998; unpublished results). A similar characteristics should apply to adults because within individuals plumage displayed at the nestling and subsequent stages has a similar coloration (Roulin, 1999a).

2 A reddish-brown plumage enhances foraging success and in turn reproductive success. This hypothesis cannot be rejected because small mammals are known to detect and escape more rapidly from visible than cryptic predators at night (Clarke, 1983; Kotler *et al.*, 1991). If

dark owls are less detectable to small mammals, they may be selected to invest more effort in reproduction than light coloured ones. If this is the case, one should find a similar covariation between plumage coloration and reproductive success in other barn owl populations.

3 The covariation between plumage coloration and reproductive success is the outcome of historic and geographical processes. After the last glaciation period barn owls invaded Europe from East to North (reddish-brown subspecies *T. a. guttata*) and from Spain to Central Europe (light coloured subspecies *T. a. alba*) (Voous, 1950). As in the northern parts of Europe clutch size is significantly larger (Table 3) and survival prospects lower (Table 4), *T. a. guttata* may have been under selection to feed their brood at a higher rate than *T. a. alba*. In this scenario, the two subspecies may have evolved different life-history tactics with more reddish-brown owls investing more effort in reproduction. This implies that when the two subspecies face similar environmental conditions in France or Switzerland, it becomes possible to detect a covariation between reproductive success and plumage coloration. Under this hypothesis, plumage coloration per se does not influence reproductive success. Therefore, in the absence of similar historic and geographical processes reproductive success and plumage coloration should not covary on other continents.

Whatever the mechanism explaining why reddish-brown males achieved a higher reproductive success, it remains to be discovered how a light-coloured plumage still persists. Two potential hypotheses can be developed here. The first one postulates that if females gain direct fitness benefits by mating with reddish-brown males, they should gain indirect fitness benefits by mating with light coloured males. This hypothesis has not yet received empirical support given that parasite resistance and immunocompetence were found to covary with female plumage spottiness (Roulin *et al*., 2000; 2001) but not with male plumage coloration (Roulin, unpublished results). The second hypothesis is based on the idea that plumage coloration is a selectively neutral subspecies genetic marker and has no effect on foraging

Table 3 Literature survey of clutch size in relation to latitude on the European continent. Pearson correlation between clutch size and latitude is $r = 0.53$, $n = 23$, $P = 0.009$.

Country	Region	Latitude	Period of study	Mean clutch size	Sample size	Author
Spain	Valencia	39.3	1989–1995	4.47	38	Martinez & Lopez (1999)
France	Jura	46.7	1981–1986	5.62	302	Joveniaux & Durant (1986)
France	Côte d'Or	47.3	1971–1979	6.01	481	Baudvin (1986)
France	Haute-Saône	47.6	1973–1979	4.95	130	Chanson *et al*. (1979)
France	Alsace-Lorraine	48.8	1977–1981	6.1	142	Muller (1982)
France	Haut-Rhin	48.8	1981–1996	5.7	?	Regisser (1984–1997)
Switzerland	Vaud	46.5	1975–1990	5.14	63	Henrioux & Henrioux (1995)
Switzerland	–	47	1935–1956	5.33	63	Schifferli (1949, 1957)
Switzerland	Jura	47.4	1982–1985	5.16	112	Luthy *et al*. (1985)
Czechoslovakia	Brno	49.2	1926–1980	6.31	32	Pikula *et al*. (1984)
Czechoslovakia	–	49.2	1975–1994	6.22	228	Proprach (1996)
Germany	Schwäbischen Alb	48.6	1958–1977	5.5	16	Rockenbauch (1979)
Germany	Saarland	49.2	1972–1977	5.23	43	Bethge and Hayo (1979)
Germany	Warndt	49.3	1973–1978	5.18	49	Hayo (1978)
Germany	Franken	49.5	1966–1974	5.51	354	Kaus (1977)
Germany	Westfalens	51.2	1990	6.22	55	Graef (in Brandt & Seebass, 1994)
Germany	Saaletal	51.2	1968–1974	5.79	309	Schönfeld & Girbig (1975)
Germany	DDR	51.4	1950–1953	5.77	146	Hummitzsch (in Schneider, 1977)
Germany	DDR	51.4	Before 1977	5.95	26	Schneider (1977)
The Netherlands	–	52.4	1969–1974	4.2	477	Braaksma & Bruijn (1976)
Denmark	–	53.5	?	5.55	74	Trap Lind (in Baudvin, 1986)
Sweden	Schonen	55.4	1962–1966	4.63	33	Frylestam (1971)
Sweden	Scanie	55.4	1959–1976	5.73	56	Holmgren (1983)

Table 4 Literature survey of the percentage of ringed birds found dead in their first-year of life in relation to latitude on the European continent (Pearson correlation is $r = 0.60$, $n = 13$, $P = 0.03$).

Country	Region	Latitude	Period of study	Total number found dead	Number found dead before first-year of age	(%)	Author
Spain	–	40.0	–	27	16	59.3	Martinez & Lopez (1995)
Switzerland	–	47.0	1952–1957	330	184	55.8	Schifferli (1957)
France	Côte d'Or	47.3	1971–1979	320	237	74.0	Baudvin (1986)
France	Haute-Saône	47.6	1962–1986	146	98	67.1	Chanson *et al*. (1988)
France	–	47.5	1935–1983	829	584	70.0	Giraudoux (1985)
Germany	South	48.0	1946–1981	1245	859	69.0	Bairlein (1985)
Germany	North	50.0	1909–1991	4786	Not given	73.0	Bairlein & Harms (1994)
Germany	Wüttemberg	48.8	1937–1954	760	501	65.9	Sauter (1956)
Czechoslovakia	Brno	49.2	1926–1980	44	29	65.9	Pikula *et al*. (1984)
DDR	Saaletal	51.2	1968–1974	138	89	64.5	Schönfeld & Girbig (1977)
The Netherlands	Liemers-Achterhoek	51.6	1967–1984	133	91	68.4	de Bruijn (1994)
The Netherlands	–	52.4	1969–1974	353	253	71.7	Braaksma & Bruijn (1976)
Sweden–Denmark	–	56.0	1962–1966	83	62	74.7	Frylestam (1971)

success. In this case, plumage polymorphism and clinal variation in plumage coloration may be stable because a high reproductive effort is selected against in southern Europe, whereas a less intense reproductive effort is selected against in northern Europe. Therefore, light coloured owls could not invade northern populations and reddish-brown owls could not invade southern populations. Under this hypothesis, clinal variation in plumage coloration (Voous, 1950) would be stable and reflects clinal variation in reproductive tactics that are evolutionarily stable. Obviously, further investigations are required to understand how polymorphism in plumage coloration is maintained in Central Europe, and also in world-wide populations.

Why does female plumage spottiness signal female quality?

With respect to plumage spottiness, sexual selection appears to be exerted on females (Roulin, 1999b; Roulin *et al*., 2000, 2001), which is an unusual situation in birds (Andersson, 1994). Four mechanisms have been proposed to explain why females rather than males should be the sexually selected sex. In the following, we review them and discuss which one may play a role.

1 Sexual selection on females is expected to occur when the sex-ratio among potential breeders is female biased. This prediction arises from the fact that under such circumstances each male could choose a partner among several females and thus exert sexual selection (Clutton-Brock & Parker, 1992). This possibility seems unlikely because both female and male barn owls are mature at 1 years of age (Roulin *et al*., 1999), brood sex-ratio at fledging does not depart from unity (unpublished results), and mortality at least because of traffic is female-biased (Massemin *et al*., 1998).

2 The sex that is under sexual selection should vary in quality to a larger extent than the choosy sex (Owens & Thompson, 1994). Thus, in the case females vary in quality to a larger extent than males, males should be selected to desert poor quality females, as the likelihood to find a prospective mate of greater quality is non-negligible. This hypothesis may apply to the barn owl because the offspring's ability to resist parasite covaries with female plumage spottiness but not with male plumage spottiness (Roulin *et al*., 2000, 2001). This suggests that the variation in parasite resistance is greater among females than males.

3 The cost of being choosy should be larger in the sex that is under sexual selection (Johnstone *et al*., 1996). For instance, if the opportunity to find another mate after leaving a prospective mate is greater for males than females, males would be expected to exert sexual selection on females. This possibility can not be excluded because barn owls begin searching for a mate in winter (Roulin, 1998), suggesting that a long time is required to find a mate, and thus that mate choice is costly and not always successful (Roulin, 1996).

4 The sex that contributes more to reproductive success should exert sexual selection on the other sex in order to avoid investing in reproduction with a poor quality mate (Trivers, 1972). This possibility is plausible because male

barn owls invest more energy in the feeding of the progeny (Roulin, 1999b). Further support is given to the prediction that males invest more than females per breeding attempt by the observation that females produce a second annual brood more often than males because they can desert their brood half way through the rearing period (Roulin, unpublished results). Therefore, variance in reproductive rate appears to be greater in females, a condition that has been proposed to favour males exerting sexual selection on females (Clutton-Brock & Vincent, 1991).

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Supplementary material

The following material is available from http://www.blackwell-science.com/products/journals/suppmat/JEB/JEB274/JEB274sm.htm

Geographical distribution and sample size of the *Tyto alba alba* populations, *Tyto alba* subspecies and *Tyto* species considered in the present study. Number of owls measured in 44 museums.